Notes on the Histriobdellidæ.

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With Plates 11—14 and 1 Text-figure.

INTRODUCTORY.

THE publication by Shearer in 1910 of an elaborate account of the anatomy of Histriobdella homari (9) has greatly added to our knowledge of that remarkable and interesting animal, which had remained neglected, so far as published work is concerned, since 1884, when Foettinger published his valuable observations on it (3).

In 1900 I published (6) an account of an allied fresh-water form—Stratiodrilus tasmanicus—which I found in the gill-cavities of freshwater crayfishes in Tasmania. Some years ago I found another member of the same group inhabiting the gill-cavities of Astacopsis serratus in streams at elevations of 2000 to 3000 feet in the Blue Mountains of New South Wales; and I have since found specimens of the same form on crayfishes from creeks of various other parts of the same river-system (the Hawkesbury)—the Cataract River and the Loddon River—from small streams flowing directly into the sea on the coast of Illawarra, at Port Hacking (Waterfall Creek, a branch of the Port Hacking River), creeks running into Middle Harbour, Port Jackson, and at Pitt Water off Broken Bay (mouth of the Hawkesbury). I have also found it in the large crayfishes

of the Murrumbidgee River of the great Murray River system, which extends over all New South Wales with the exception of the narrow strip between the Dividing Range and the coast, over southern Queensland and a good part of Victoria and a small part of South Australia. The range of Stratiodrilus would thus appear to be very extensive. So far, in continental Australia, I have found it only on the spiny crayfish (Astacopsis serratus), never on Chæraps bicarinatus,[1] on specimens of which, from widely sundered localities, I have carefully searched for it.

A re-comparison of Stratiodrilus with Histriobdella with the aid of Shearer's paper and with the help of specimens of the European form,[2] shows that the two, though closely allied, are yet very distinct in a number of points. Stratiodrilus is a distinctly more highly-organised animal, as is shown in the more highly differentiated muscular and nervous systems, and in the presence of the three pairs of cirri with their sensory cilia. The excretory system of the two genera is widely different, as will be pointed out subsequently. Other points of difference are the following : The tentacles in Histriobdella are unjointed; in Stratiodrilus they are all two-jointed. The anterior limbs are non-retractile in Histriobdella; freely retractile in Stratiodrilus. Histriobdella has no definite tail region; in Stratiodrilus this region is sharply marked off from the trunk, and its body-cavity is cut off from that of the latter by a partition. A further difference lies in the position of the mouth, which in Stratiodrilus is further forward than in Histriobdella.

The Australian form is nearly related to the Tasmanian. I

[1] In a useful and suggestive paper (' Proc. Zool. Soc.,' 1912) on the Australian crayfishes, Geoffrey Smith proposes to separate the bicarinate crayfishes from the other smooth crayfishes under the new generic name of Parachæraps.

[2] I found them common in Nephrops norvegicus. I have pleasure in thanking Prof. Cossar Ewart, Dr. J. H. Ashworth, and Prof. J. P. Hill for kind assistance.

propose for the former the name Stratiodrilus novæ-
hollandiæ. The chief differences are in the jaws and,
perhaps, the excretory system. The jaws are usually con-
siderably longer in proportion to the size of the head, so that
when retracted they project backwards some distance into
the following or "neck"-segment. In the minute structure
of the jaws with their teeth there are also some constant
points of difference, which will be referred to later. There
is also a difference in the form of the chitinous penis as shown
in figs. 20–25. In S. tasmanicus it has its three basal
processes more widely spread and is thinner at the base than
in S. novæ-hollandiæ.

I prefer to postpone any further attempt to determine the
relationships of the Histriobdellidæ with other groups of
animals until I am in a position to give an adequate account
of the development of Stratiodrilus, for which I have
now obtained a good deal of material.

External Features of Stratiodrilus; Movements.

Stratiodrilus novæ-hollandiæ is of similar size to S.
tasmanicus (about 1 to 1·5 mm. when full grown), and
resembles it closely in both external features and internal
structure. It consists of a head, which is a little less than a
sixth of the total length, five body-segments, and an imperfectly
segmented tail region. The first of the body-segments, which
is shorter than the others and bears no cirri, may be dis-
tinguished as the neck-segment. As in S. tasmanicus, the
second, third and fifth segments bear each a pair of two-
jointed cirri, both of which are provided with non-motile
sensory cilia. The head bears the same appendages as in
S. tasmanicus, viz. a median tentacle, two pairs of lateral
tentacles and a pair of retractile anterior legs. The tentacles
are all on the average relatively shorter than in the
Tasmanian form, more especially those of the second lateral
pair. The fourth segment in both species bears no append-
ages in the female, while in the male it bears the retractile

claspers, which are of essentially the same character in both. The posterior limbs do not differ in any essential feature in the two species, except that the cirrus (figs. 18 and 19) with which it is provided is divided into two segments by means of a joint like the other cirri, the corresponding appendage in S. tasmanicus being undivided.

With a close agreement in structure between the Australian (continental) and Tasmanian forms there is associated a correspondingly close resemblance in movements and general mode of life (see 6, p. 303). In ordinary locomotion the anterior limbs are usually completely retracted, progression being effected exclusively though the peculiar "walking" movements of the hind limbs. Frequently the animal remains for a long time fixed by means of the hind limbs, the body being either extended flat on the surface, the head groping about with the tentacles and occasionally "grazing" on the substratum by series of rapid movements of the jaws, or assuming a half-erect position with the tentacles flexed towards the dorsal side.

Stratiodrilus is able to walk in a reversed position by means of the surface film of the water. But much more remarkable is its ability to progress in mid water. The movement can hardly be described as swimming : slow locomotion through the water is effected by deliberate alternate movements of the hind limbs, as when the animal is progressing on the surface of a solid object. This was observed only in water clouded with suspended flocculent particles.

Though the usual habitat of Stratiodrilus is the gill-cavity of its host, specimens are sometimes found on the outer surface. Probably this only occurs under abnormal conditions.

Like Histriobdella, as stated by Shearer (9, p. 297), Stratiodrilus readily deserts its host when conditions are in the least abnormal. When the crayfish is kept for a little time in a vessel with a limited amount of water, Stratio-drili will frequently be found crawling on the bottom of the

vessel, and it often happens that under such circumstances none are to be found in the branchial chambers.

Body-cavity.

Surrounding the enteric canal, between the wall of the latter and the wall of the body, is a space of considerable size, which occupies the position of the cœlomic cavity of the Annulata. This is referred to by Fœttinger (3, p. 490) as the "cavité générale du corps," and is described by him as a cavity between the musculo-cutaneous tube and the digestive— bounded by somatopleure and splanchnopleure, which are stated to be thin cellular membranes with flattened nuclei. A corresponding cavity in the head is said to be completely cut off from the body cavity of the trunk by a septum composed of large cells. The somatopleure of the trunk is described as clothing the dorsal and ventral muscles and the nerve-cord.

Shearer (9) terms the cavity in question blastocœlic cavity on the assumption that it corresponds developmentally with the similarly situated cavity in Dinophilus, and that the latter is of blastocœlic derivation. He describes prolongations into the head and into the posterior limbs. He doubts the correctness of the view that it is lined by a cœlomic epithelium.

The gut surface, he admits, is lined by a delicate "cuticle" with small flat nuclei at rare intervals, and he maintains that it is difficult to say if this is a membrane or a "mere secretion from the blastocœlic ends of the cells of the gut-wall." The somatopleural side of the cavity, he asserts definitely, is not lined by any such membrane : the longitudinal muscles, as in Stratiodrilus, are surrounded by a delicate cuticle similar to that which lines the outside of the gut, but no nuclei are to be seen in it. He maintains that neither the splanchnic nor the somatic layer is of the character of a true peritoneal or cœlomic epithelium.

I have not yet been able to work out definitely the

development of the corresponding cavity in Stratiodrilus, but what evidence I have before me seems to point rather to a schizocœlic origin than a blastocœlic derivation. However this may be, the layer which forms its splanchnic boundary is assuredly of the nature of a nucleated membrane. The presence of the nuclei, though there are wide intervals between them, definitely proves untenable the view that this layer can be looked upon as a cuticle or as a secretion from the cells of the enteric epithelium. The somatic layer also is in a part of its extent quite unmistakeably a membrane of similar character. Forming the ventral wall or floor of the body-cavity is a thin membrane of material similar to that which forms the splanchnic layer, and with similar flattened nuclei. On the dorsal side this membrane does not exist, and the nuclei, if represented at all, are represented by nuclei which lie embedded in protoplasm on the inner surfaces of the muscular fibres.

To avoid the misconception that in this substance lying between the epidermis and the enteric epithelium we have to do with a definite epithelium, I propose to use the term cœlenchyme introduced by Salensky, and applied later by de Beauchamp (1) to a very similar tissue occurring in Dinophilus. The cœlenchyme is to be found in what is probably its most significant, because its most primitive, condition in the tail region (fig. 15 c. and figs. 2–6 c. c.). Here, as in the trunk, it forms a definite splanchnic layer surrounding the enteric epithelium of the intestine. But there is no distinct somatic layer. Instead there is on either side an irregular strand running forwards from the corresponding rectal gland, and connected with its fellow of the opposite side by a transverse strand, which is intimately united with the dorsal surface of the nerve-cord. In each of the lateral strands runs the caudal part of the corresponding third nephridium. From each lateral strand branches are given off which become continuous with the longitudinal muscular fibres, both dorsal and ventral—a nucleus occurring in each of these branches close to its termination in the muscular fibre. On

each side the branches to the dorsal fibres are given off from an almost vertical lamina, through the ventral part of which the nephridium runs. Enclosed between these two laminæ on the ventral side of the intestine is a longitudinal channel, which forms the chief part of the body-cavity in this region. Further forwards, towards the anterior limit of the caudal region, the laminæ of the cœlenchyme become exceedingly thin, and the branches passing to the dorsal series of muscular fibres appear as offsets from the splanchnic layer, those to the ventral fibres being, as before, given off from the main longitudinal strand in which the nephridium runs.

At the point where the tail passes into the trunk the relations of the cœlenchyme and the muscular fibres become somewhat complicated owing to the development of an oblique septum, partly muscular, dividing the body-cavity in this position; and in the reproductive segments in front of this a similar degree of complication is brought about in the female by the presence of the large ripe ovum, and in the male by that of the penis, accessory glands and vesiculæ seminales.

In the male in the posterior part of the genital region the most considerable part of the cœlenchyme takes the form of a pair of wing-like, nearly horizontal, lateral plates projecting out from the splanchnic layer covering the intestine, and giving off branches to the dorsal muscular fibres. The cœlenchyme does not here form a continuous somatic layer on either surface. Further forwards there are formed a pair of vertical partitions, partly muscular, separating off a median chamber containing the intestine, the nerve-cord, the penis and a median part of the testis, from two lateral chambers enclosing the lateral portions of the testes, the vesiculæ seminales and the prostate glands. In this part the cœlenchyme only gives rise locally and imperfectly to a somatic layer. The splanchnic layer is reflected over the testes, etc.

In the female the posterior part of the genital region is so distended by the enormous ripe ovum (fig. 10) that the other parts become reduced and compressed, and the cœlenchyme

is condensed to form definite somatic and splanchnic layers, the former closely applied to the muscular layer of the body-wall, the latter giving rise to an investment for the ovary in addition to the usual layer investing the narrowed intestine, here sunk in the dorsal body-wall.

Further forwards (fig. 9) a pair of vertical longitudinal septa are formed very much as in the male, the median chamber enclosed by them being occupied by the intestine, the nerve-cord, and the ends of the loops of the third pair of nephridia, the lateral chambers lodging the lateral parts of the ovaries. The median chamber is crossed by strands of cœlenchyme, the most constant of which is one that forms a horizontal partition bounding dorsally a channel (partly divided by a median vertical partition) running immediately above the nerve-cord. The somatic cœlenchyme here forms a definite membrane on the ventral side; a splanchnic layer invests the ovaries.

In the anterior trunk region (fig. 7) the vertical septa become replaced by oblique septa (of cœlenchyme with occasional muscular fibres).

These extend from the middle of the dorsal body-wall, and run outwards and downwards, holding the stomach between them as they diverge, and are inserted into the lateral parts of the ventral surface. There is a continuous somatic layer on the ventral side closely related to the ventral longitudinal muscles, circumscribing them into two distinct bundles.

The body-cavity extends through the neck-segment into the head (fig. 13 and figs. 1 to 6). Septa of cœlenchyme with muscular fibres which run nearly transversely separate the cœlom of the neck-segment from the cœlom of the head in front ($S.$ 5) and from that of the first trunk-segment behind ($S.$ 1). Whether these form complete partitions is doubtful. The fact, recorded in my previous paper, that spermatozoa occur sometimes in the interior of the head-cœlom is not conclusive as to the existence of apertures in the septa, since the sperms might have been directly injected into the head. The neck-cœlom, certainly, under certain circumstances, as

described below in the account of the cervical glands, behaves like a closed cavity. In the head the cœlom is represented by an extensive cavity on the ventral side, with lateral extensions round the jaws and their muscles, opening dorsally into a considerable median cavity situated beneath the brain. These head-cavities are quite clear except for some muscular fibres. They have a splanchnic layer of cœlenchyme like that covering the intestine, forming a capsule enclosing the jaws and their muscles, and the existence of a parietal layer is indicated by the presence of very sparsely distributed nuclei.

Briefly stated, the arrangement of the cœlenchyme and its relations to the cœlom in Stratiodrilus are as follows: The cœlom, which is probably a schizocœle, is not lined in any part by an epithelium; but the cœlenchyme, a nucleated substance of undifferentiated, finely fibrillated material, with no trace of division into cells, partly takes the place of such a membrane. It forms a thin splanchnic layer investing the whole of the digestive canal and the ovary and testis. Its somatic portion, which assumes the character of a continuous layer on the ventral side only, is intimately connected with the longitudinal muscular fibres of the body-wall, of which it constitutes the formative (myoblastic) material.

As I pointed out in my previous paper, this condition, in which the same elements play the part of myocytes and of somatic cœlomic epithelium, is essentially not dissimilar to the condition in the larva of Polygordius (Fraipont, 4), in which a single layer of cells gives origin both to the longitudinal muscular fibres and the somatic layer of the cœlomic epithelium. To judge from certain of Eisig's figures (2), the same holds good of the Capitellidæ.

Pierantoni (8) describes a complete peritoneal layer in Protodrilus, but does not enter into an account of its relationships to the muscular layers. In his text-fig. 1, p. 33, he shows a cell with a flattened nucleus lying within and distinct from the protoplasmic parts of the longitudinal muscular fibres, and refers to it as representing the peri-

toneum. From this we might infer that a distinct separate layer of such cells lines the cœlom, but the figures of sections given in the plates—e. g. the figures on Pl. 7—do not show this, and represent only a single set of nuclei.

But there are also adult forms among the Chætopoda in which the condition is remarkably like that occurring in Stratiodrilus. In an Enchytræid not yet determined, which is very common in Sydney in moist garden soil, there is, as represented in fig. 29, in many parts only one layer, not composed of cells, but of a nucleated material which is not unlike the cœlenchyme of Stratiodrilus, doing duty both as the myocytes of the longitudinal muscular fibres and also as the somatic cœlomic layer. But in some parts this material is divided into two layers—an outer, surrounding the inner edges of the muscular fibres, and containing nuclei situated in close contact with the latter, and an inner, provided with nuclei flattened tangentially, situated at irregular intervals. The substance of these two layers is in great measure in continuity, the filaments of the protoplasm being traceable from one to the other, and in some parts the coalescence appears to be complete, so that only one layer is recognisable.

In this Encytræid, then, the relations of the somatic peritoneal layer are either more primitive than in the Oligochæta in general, or have become secondarily modified, and are closely comparable to what occurs in Protodrilus, approximating to a certain extent towards the condition prevailing in the Histriobdellidæ (fig. 28). It seems to me highly probable that in this respect, as in the relations of the nervous system to the epidermis,[1] the more primitive, or simplified, condition may prove to be by no means exceptional among the smaller and simpler Chætopoda.

Jaws and Digestive System.

The jaw - apparatus of the Histriobdellidæ is an extremely complex structure. Altogether some thirty distinct

[1] See E. S. Goodrich, " On the Structure and Affinities of Saccocirrus," 'Quart. Journ. Micr. Sci.,' N.S., vol. 44, p. 422.

chitinous pieces with elaborate articulations enter into its composition. It is thus a much more complex structure than the mastax of certain Rotifers to which I have compared it. Yet the resemblances to the "malleate" form of mastax are very striking, and are worthy of notice in connection with the question of the phylogeny of the Histriobdellidæ.

Compared with the typical malleate mastax, as we find it exemplified in Brachionus, the jaw-apparatus of Stratio-drilus is found to differ in the following chief points:

(1) The fulcrum is produced into a long slender rod.

(2) Each ramus is represented by four more or less parallel jointed rods or ramules, each of which bears terminally one of the four complex teeth which represent the uncus.

(3) The uncus is thus essentially related, not to the manu-brium, but to the ramus.

(4) The manubrium is probably represented by a very slender rod which articulates with the ramus towards its distal end and extends outwards.

(5) The lower jaws of the Histriobdellidæ are apparently not represented at all in the mastax of the Rotifer, unless we are to look on them as corresponding to greatly developed posterior parts of the manubria.

(6) The entire apparatus, it is important to note, is situated, not in the interior of the enteric canal as in the Rotifer, but in a blind pouch (pharynx) which lies on the ventral side of the œsophagus and opens on the exterior through the mouth. In Paraseison alone among the Rotifera does the mastax occupy a corresponding position.

I am able to supplement my earlier account of the jaws of Stratiodrilus by certain additional particulars regarding the rami of the upper jaw and to give more detailed figures of them (figs. 26, 27). Each ramus consists of four sets (ramules) of movably articulated chitinous pieces, each ramule ending in a "tooth." Of these four teeth only the outer two have the curry-comb-like character to which I previously directed attention (6, p. 307). The other two are

beset on the inner aspect with a row of sharp denticles, four in number on the outer tooth, eight on the inner. All four ramules of each ramus are connected together by articulations, so that they act together in the movements of protrusion and biting.

The jaws of S. novæ-hollandiæ differ from those of S. tasmanicus in certain respects. In most cases, as already mentioned, the entire apparatus is considerably longer in the former than in the latter. The individual chitinous parts also present definite and constant differences. The most marked of these concerns the broad plate which terminates each of the lower jaws in front. The anterior margin of this plate, provided with about six irregular denticulations in S. tasmanicus (fig. 16), is in S. novæ-hollandiæ (fig. 17) marked with a deep, rounded incision near its inner margin, followed by a comparatively large tooth, which is separated by a shallow notch from a second, much smaller tooth.

The muscles of the jaws have been described in Histriobdella by Shearer and in Stratiodrilus by myself, and the agreement between the two genera is fairly close. The chief muscles in Stratiodrilus are in three sets. One of these represents what Shearer calls in Histriobdella the "bulb-like muscular organ of the jaws." In Stratiodrilus I described it as "a pair of large bundles of non-striated fibres, each of which is wrapped round the ventral side of the corresponding lower jaw, the fibres running forwards parallel with the latter throughout their (its) length. These two muscles are in close apposition with one another along the mid-ventral line, separated, however, by a thin septum of nucleated material continuous with the lining of the head cœlom, of which it appears to be a thickening. They are continuous with the retractor fibres behind. The ventral edge of each is unfolded, and becomes continuous with the ventral edge of the corresponding muscle of the second pair "—to which account has to be added the statement that these muscles are continued from the lower jaws almost vertically upwards to

the dorsal wall of the head, embracing between them the œsophagus and the dorsal cephalic gland (fig. 13). In the living animal, when the fibres of these muscles contract, there are synchronous movements of the margins of the mouth.

The second pair are the striated muscles (figs. 2 and 13, *s. m.*), the fibres of which arise from the shaft of the lower jaw towards its posterior end and run straight forwards to be inserted into the corresponding bridle—a curved chitinous piece that slides backwards and forwards along the shaft and probably serves as the medium through which the contractions of the striated tissue are transmitted to the rami of the upper jaw (see **6**, p. 309).

A third set of muscular fibres arise from the fulcrum of the upper jaw, and run forwards parallel with it to be inserted into the rami. These apparently bring about restricted biting movements which sometimes occur when the entire jaw apparatus is not fully exserted, the chief biting movements, with the jaws in a state of complete protrusion being probably due to the contractions of the striated muscles inserted into the bridles.

A number of muscular fibres arising from the wall of the head in the posterior part of its extent about the bases of the anterior limbs pass through the cœlomic space that underlies the brain, partly in relation to its dorsal, partly to its ventral, surface, and are inserted into the rami. In addition, retractor and protractor strands pass to the apparatus from the walls of the head.

The digestive system is much the same in essentials in Histriobdella and in Stratriodrilus. The whole system, apart from the jaws and certain glands to be referred to presently, consists of a simple tube (figs. 1 to 6) running straight through from mouth to anus. The first part, the œsophagus, situated in the head, is an extremely narrow tube. The second part, stomach, running through the anterior trunk region, is much wider. Then follows a very narrow anterior part of the intestine running through the reproductive seg-

ments, and finally a wider intestine running through the tail region and terminating in the anus at its posterior end on the dorsal side. The wall of the canal consists throughout of a single layer of comparatively large cells ciliated internally and a thin investment of the splanchnic cœlenchyme, already referred to. Here and there is a cell which responds much more intensely than the rest to staining agents, and which may perhaps be differentiated as a secretory cell.

Connected with the œsophagus are a pair of glands (figs. 2–5, *gl. c.*), not hitherto noticed which from their position may be termed the c e r v i c a l   g l a n d s. These are situated in the neck-segment at the sides of the œsophagus in the interval between the jaws in front and the intestine behind. In the living animal they appear as somewhat conspicuous objects owing to their greenish colour, but a very slight pressure causes them to become broken up, when the green matter becomes diffused through the space (cœlom of neck segment) bounded by transverse septa in front and behind. Each gland is triangular in outline when looked at from above or below, one angle being internal and the other two external. The internal angle is in close apposition with the narrowest part of the œsophagus, where it passes into the intestine. In section the gland appears very finely fibrillated, not showing any trace of division into cells, with only a small number of nuclei placed at wide intervals. In one series of sections the gland appears to be unicellular with a single large nucleus, larger than any others that occur in the head-region, with a definite spherical nucleolus; any other nuclei towards the periphery belonging to other elements. In other series this point is not so distinct. The two glands are closely applied together below the œsophagus, separated by a very fine median vertical fissure. Closely applied to their ventral surfaces are the transverse parts of the first or cephalic pair of nephridia, and between this surface and the ventral body-wall is a distinct space—the cœlom of the neck-segment (fig. 1, *ce. c.*).

Comparison of series shows that these glands are essentially

unicellular, but may become plurinuclear by division of the original single large nucleus. The bodies above described are not referred to either by Fœttinger or by Shearer, though they are distinctly shown in the figures of longitudinal sections by the former. They are entirely distinct from the salivary glands of the latter author, which also occur in Stratiodrilus, and lie further forwards in close relation to the jaws and their muscles. Their physiological connections may be with the nephridial and not the digestive system.

Another conspicuous structure in this region, not represented or not recognised in Histriobdella, lies on the dorsal side of the head, a little further forward. This is a median organ (figs. 4 to 6 and 13, *gl. d.*), deeply divided behind into right and left lobes, which lie at the sides of the œsophagus, and are thus dorsal to the jaws. The unpaired part very closely invests the dorsal surface of the œsophagus. In front it becomes divided into three distinct lobes, giving off dorsally narrow processes, which end in the epidermal layer.

The nature of this organ—the dorsal gland—is doubtful. Its substance stains deeply with hæmatoxylin, when it presents a vacuolated appearance, suggesting that of a gland for secreting mucus. It is not divided distinctly into cells, and contains only a few nuclei, which are very similar to those of the cells of the glands belonging to the anterior limbs.

Yet another pair of glands which have not been noticed hitherto may be referred to here. These are a pair of spherical masses of cells (figs. 4 to 6, *r. gl.*), each situated at the side of the anus in close relation to the corresponding posterior limb-gland. The cells have a generally radial arrangement, but I have found no lumen, and have not been able to trace any duct, and there is no definite evidence that these glands, which may be termed on account of their position the rectal glands, have any outlet.
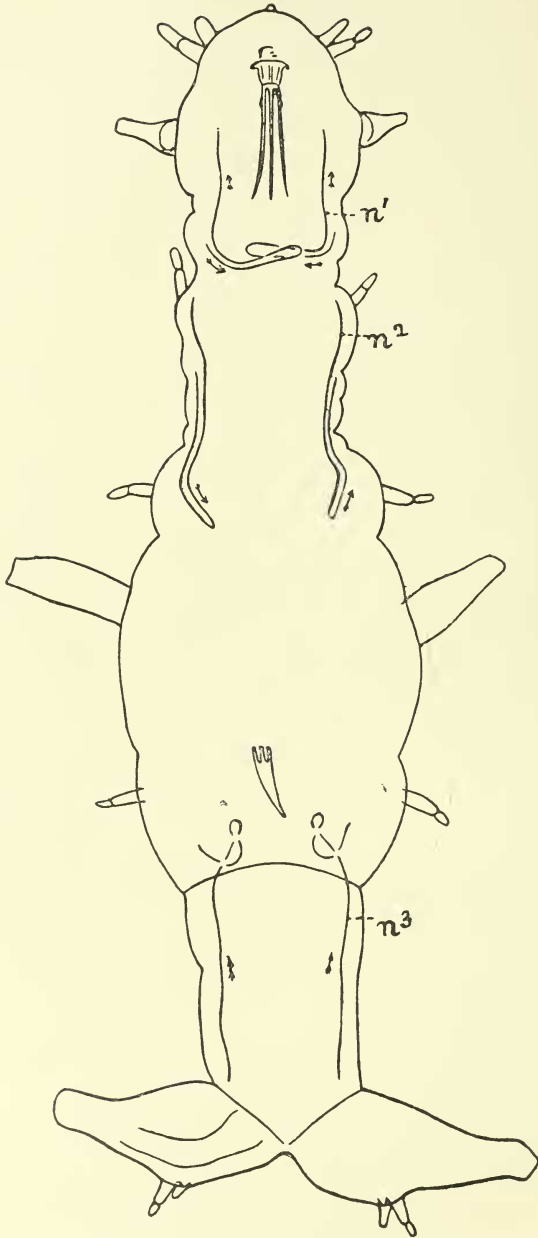
Outline of male Stratiodrilus novæ-hollandiæ to show the arrangement of the nephridia, n^1, n^2, and n^3. The arrows indicate the direction of the ciliary movement.

The Nephridia.

There are three pairs of nephridia (Text-fig. 1) in both male and female. The nephridia of the first pair (head nephridia) are alike in both sexes. Each begins in the lateral part of the neck segment, not far from the lateral border. In some series of sections each tube seems to have its origin in a thin-walled vesicle. From its point of origin the nephridial tube runs inwards with a curve, the convexity of which is directed backwards, and crosses the middle line, running ventral to the œsophagus and some little distance behind the posterior extremities of the jaws. After crossing the middle line the nephridium extends for a little distance further in the same direction, and then bends sharply round on itself, forming a complete loop, and running back almost parallel with and somewhat in front of its first-mentioned inwardly trending limb, till it reaches a point not far from the origin of the latter, when it again changes its course to run straight forward into the head. In the head the nephridium is traceable by means of its contained cilia to a point nearly opposite the middle of the base of the anterior limb, where the ciliary movement is always found to cease in a position far removed from either surface of the head. In sections the tube is traceable to a point just in front of the cephalic limb, where it comes close to the ventral surface and terminates there. It is at this point doubtless that the external aperture is situated. But apparently in this terminal non-ciliated part of the nephridium the lumen becomes divided up into a number of extremely minute channels, of which the openings on the surface would not be traceable. The wall of this nephridium is very delicate throughout, and it is in few series of sections that the arrangement can be followed. Where the loops overlap, on the ventral aspect of the neck-segment, the nephridia have the appearance of narrow channels lined by cilia running through a mass of fibrillated material, in which a nucleus is embedded here and there.

The second pair of nephridia (n^2.) begin in both sexes close
to the bases of the first pair of cirri, but dorsal to the latter;
in some cases each appears to originate in a small contractile
vesicle.   From this point each runs backwards through the
rest of the second segment and through the whole of the third.
In the male it bends inwards at a point nearly opposite the
base of the second cirrus (third segment), and, after running
inwards and backwards until it approaches very near its
fellow of the opposite side, it bends sharply round on itself a
little distance in front of the clasper.   From the bend it runs
forwards in close relation to its posteriorly running limb and
on its outer side.   The external opening of this nephridium
has not been observed in the male.   The cilia of the anteriorly
running limb cease a little distance in front of half the interval
between the first and second cirri, and the last cilia are a
considerable distance from the surface, so that the terminal
part here, as in the head nephridia, would appear to be non-
ciliated or to possess cilia that are not usually in movement.
In the female the second nephridium is continued further
back than in the male, the loop or bend (fig. 7) occurring
nearly opposite the anterior paired part of the ovary.   The
anteriorly running limb of the loop runs throughout on the
inner side of the posteriorly running limb, quite close to the
latter as seen in transverse sections, and opens on the exterior
on the ventral surface near to, and a little in front of, the
second cirrus.   In one transverse series the part near the
opening is loaded with a quantity of amorphous, opaque matter.
The terminal part is a coiled non-ciliated tube.

The third nephridia (n^3.) in both sexes begin at the
posterior end of the tail region.   In line with each, behind
the point where the lumen begins, is a row of four or five large
nuclei, situated at the side of the rectum.   It runs forwards
on the ventral side between the nerve-cord and the intestine
till it enters the trunk.   In this position the vessel is quite
distinct in thin sections (fig. 15).   In the female the trunk
part of the nephridium runs forwards on the dorsal side of
the ovary to a point near the anterior extremity of the latter,

where it bends round and runs inwards and forwards below the intestine to form a loop (figs. 8 and 9), which approaches near to or even meets that of the opposite side in a space between the intestine and nerve-cord, bounded laterally by a pair of almost vertical septa and separated from a space immediately overlying the nerve-cord by a horizontal septum. The returning limb of the loop is dorsal and, further back, internal to the other ; it runs back, and is traceable as far as a point nearly opposite the third cirrus and about half way between the lateral border and the middle line. Its external aperture on the ventral surface must be a little behind the third cirrus, but the absence of cilia in the terminal part makes it difficult to fix this point definitely, and this part of the nephridium, owing apparently to the crowding produced by the presence of the reproductive apparatus, is extremely hard to follow even in the best series of sections.

In the male the trunk portion of the third nephridium forms a loop which does not extend as far forward as the penis and seminal vesicle. The returning limb of the loop, which may be twisted on itself, passes towards the ventral side and the cilia terminate a little distance behind the base of the third cirrus.

The above account of the nephridial system of S. novæ-hollandiæ differs in certain important points from that which I have previously described as the arrangement in S. tas-manicus—particularly as regards the first and second pairs. Whether these discrepancies are due to actual differences in the two species, or, as seems more probable, to misinterpretation of the appearances previously observed, can only be determined by the re-examination of the Tasmanian species in the living condition.

The differences between the nephridial system of Histriob-della as described by Foettinger (3) and more recently and more fully by Shearer (9), and that of Stratiodrilus are of a very marked character. In the former the system does not extend either into the head or into the tail, and the three (♀) or four (♂) pairs of tubes of which it is composed are simple,

approximately straight, and run in all cases from before back-
wards to open on the ventral surface.

In the occurrence of a pair of nephridia in the head region
in the adult condition, Stratiodrilus differs not only from
Histriobdella, but from every other group with which it
might be supposed to have affinities. The extension of each
of these head-nephridia in a loop across the middle line is also
a very special feature. Perhaps this may be explained by the
very intimate relationship that appears to exist between these
loops and the structures which I have called the cervical
glands, and which, as I have already suggested, may belong
to the nephridial system.

Both Foettinger and Shearer describe the nephridia as
intra-cellular tubes, and the former definitely states (p. 471)
that the section has the appearance of a rounded nucleated
cell presenting an aperture in its cytoplasm. But such a
description does not convey an accurate impression of the
actual nature of these organs—at all events as they occur in
Stratiodrilus. The tissue through which they run is not
cellular in the strict sense of the term. It consists of a
differentiated part of the nucleated cœlenchymatous tissue
not divided into cells, the outer portion of which has the
function of the myoblastic tissue for the muscular fibres of
the body, while the inner forms a thin layer investing the
gut and having the relations, though not the structure, of a
splanchnic epithelium. Throughout a whole series of sections
of the caudal region there are no nuclei that have any special
and intimate relationships with the walls of the nephridial
tubes. Further forwards in the same pair of nephridia, where
the walls have assumed greater definiteness, and where, at
long intervals, nuclei appear in this wall, there is still no
question of cells, but simply of a greater condensation of the
tissue around the lumen of the nephridia.

Foettinger describes the vibratile structures in the interior
of the nephridia as cilia. But, as Shearer has pointed out,
they have much more the appearance of elongated flagella.
The relationships of these are very difficult of determination,

and, in common with Shearer, I find myself quite unable to come to a decision as to their connections.

Nervous System.

The remarkable development of the nervous system in the Histriobdellidæ, and especially in Stratiodrilus, distinguishes them widely from any lower group with which we can compare them, and, if not constituting strong evidence of annulate affinities, is a very remarkable instance of convergent development. In Histriobdella this system was described with great thoroughness and completeness by Foettinger, and additional details were given by Shearer, and a careful comparison with the nervous system of Dinophilus gyrociliatus as described by Nelson (7).

The nervous system of Stratiodrilus novæ-hollandiæ closely resembles that of S. tasmanicus. The cerebral ganglion (figs. 2 to 6, *b.*) contains a massive neuropile situated in the head towards the dorsal surface, somewhat in front of the middle of the region and well behind the mouth. In sagittal section this appears ellipsoidal in outline, with a slight dorsal depression indicating a division into anterior and posterior lobes. In horizontal section it is seen to be somewhat more elongated transversely than antero-posteriorly, and to be divided by a wide posterior notch into two lateral lobes. Applied to the neuropile dorsally and laterally are a great number of nerve-cells. These extend over the greater part of the head, and are continued backwards for some distance along the œsophageal connectives. This layer of nerve-cells is distinct from the epidermis, which is continued as a definite layer, with an occasional characteristic nucleus, between it and the surface. At the same time it lies distinctly outside the neuropile, and thus the appearance which the brain as a whole presents in sections is very characteristic, and differs in a very marked manner from the appearance presented by corresponding sections in the case of a Chætopod. Probably in this, as in so many other points, there is a closer connection

with Dinophilus than with any other annulate animal (see Nelson, 7, pl. 13, fig. 20).

Opposite the base of each of the tentacles is a group of nerve-cells which give off processes outwards into the tentacle and inwards into the neuropile.

There is a distinct rudimentary visceral nervous system (fig. 13, *v. n.*) similar to that described by Foettinger as occurring in Histriobdella. It consists of a pair of strands of nerve-cells given off from the œsophageal connectives close to their origin from the brain and passing back to the jaws and their muscles.

The œsophageal connectives pass downwards and backwards at the sides of the œsophagus and jaws to meet towards the ventral side of the neck-segment in the first ganglion of the ventral chain. Each gives off, as above stated, close to its origin from the brain a visceral nerve, which, accompanied by a number of nerve-cells, runs backwards among the muscles of the jaws.

The first ganglion of the ventral chain (figs. 1-6, *n. c.*), situated in the neck-segment, is a very small one and is scarcely separated from the next. The ganglion of the second segment is of large size, and extends throughout the greater part of the length of the segment. Throughout the greater part of the length of the second segment the nerve-cord is double, being divided by a median vertical fissure, which is continued into the connective between the second ganglion and the third. Laterally the second ganglion gives off a pair of nerves, passing to the small ganglia at the bases of the cirri of the first pair. The third ganglion is also a large one, and is not divided by any median fissure : it gives off the nerves to the second cirri. The connectives between the third ganglion and the fourth, which are shorter than those in front, are separated by a well-marked median fissure. The fourth ganglion in the male corresponds to the claspers, to which it gives off a large offset. In the female the corresponding nerves end in a pair of lateral ganglia. The succeeding pair of connectives are separated from one another

by a narrow, but distinct, fissure.   In the female the nerve-
cord is much compressed in the fifth segment, in which the
single mature ovum is formed.   In the male, in a correspond-
ing position in the fifth (or second reproductive) segment, the
cord bends away from the ventral surface and passes on the
dorsal side of the vasa deferentia and penis to resume its
ventral position behind them.   The fifth ganglion, the last of
the trunk, gives off nerves to the cirri of the third pair.   The
connectives following this are very short and are in close
apposition: they correspond in position to the partition
between the trunk and the tail.   In the tail region are a
series of rather small ganglia which are in very close apposi-
tion, the intervening connectives being very short and in a con-
tracted specimen scarcely distinguishable.   These five small
ganglia correspond to the five imperfect segments into which
this region is divided by slight external transverse constric-
tions.   Each of these ganglia has connected with it laterally
a pair of small ganglia corresponding serially with the lateral
ganglia in the segments of the trunk.   Posteriorly the nerve-
cord divides into two branches, one passing into each
posterior limb, each giving off a branch to the corresponding
limb-cirrus.

Reproductive System of Female.[1]

S. novæ-hollandiæ has a pair of extensive vitelline
glands (figs. 7–9, vit.) corresponding to those of S. tasma-
nicus (6, p. 322, fig. 11, vit.)   These are a pair of irregularly
shaped masses, of deeply staining protoplasmic material, partly
divided into several elongated narrow lobes, without cell-
boundaries, but with nuclei at irregular intervals.   They are
dorsally situated in close relation to the dorsal bundles of
longitudinal muscular fibres, and they extend from a point
just opposite the second cirrus throughout the greater part
of the length of the genital segments, each entering the
corresponding ovary and terminating in a leash of slender

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[1] I have nothing to add to the account previously given by me of the
male reproductive apparatus.

processes (ducts) in the neighbourhood of the posterior part of it. They do not contain any yolk-granules as such, and the latter must be formed within the growing ovum itself, the secretion providing the requisite material. That they do perform this function I conclude from their situation, and from the fact that they are the only organs of sufficient bulk to be capable of producing with rapidity the relatively considerable mass of substance which the ovum has to receive before it reaches maturity.

In mature females there is nearly always a single ovum (figs. 1–6, and 10, 11, *ov.* [1]), which is very much larger than the second in size, and which causes the distension of the region of the body in which it lies and the compression of the other organs—intestine, nerve-cord, and muscular system. The cavity in which it lies, a part of the cœlom, is situated between the cirri of the third pair. A pair of forward extensions of this cavity enclose the rest of the ovary in the shape of right and left lobes. The entire ovary is enclosed in a thin layer of splanchnic cœlenchyme, which is produced inwards in such a way as to form an investment for each of the fully formed ova. Each ovarian lobe contains a single row of ova, diminishing in size from behind forwards. This row bends inwards at the apex of the lobe, and turns back on the inner side to become merged in a nucleated layer which is not separable from the cœlenchymic investment, and in which occasional mitotic figures are to be detected.

The principal ovum is loaded with large spherical yolk-granules, and in some cases the ovum next in size contains more or fewer of these bodies; in the rest yolk-granules are absent. In sections which have been well stained with hæmatoxylin the outermost layer of the largest ovum, and usually that of the next in size, is darkly coloured by the dye, and appears as an investment of a vacuolated character sending numerous short processes inwards. This is obviously not a special investment, but a superficial protoplasmic layer having an affinity for a nuclear stain that in all other parts affects in the same degree only the nuclei.

The efferent part of the female apparatus of Stratio-
drilus differs considerably from that of Histriobdella as
described by Foettinger, whose account is endorsed by
Shearer. It was incorrectly described in my former paper,
since I mistook the returning limbs of the third pair of
nephridia for the oviducts. There are two female apertures
situated ventro-laterally a little distance behind the third
pair of cirri (fig. 14, ♀). Each leads into a short passage,
which in some cases shows a rounded dilatation. Around the
aperture, adherent to the integument, is an irregular layer
of amorphous clear-looking matter (Sh.), which may partly
block the passage itself. I am inclined to agree with
Foettinger that this must be shell-forming material, and that
it is produced by the specially developed epidermal layer
around and within the aperture; it does not possess the
resistent character of the egg-shell itself; but that would, as
in other cases, only be acquired on contact with the ovum—
probably as the result of some influence exerted by the outer
layer of the protoplasm. The passage or oviduct opens
internally into a compartment of the body-cavity bounded
behind by the septum separating the trunk-cœlom from the
tail-cœlom, and in front by a second partition of cœlenchyme
bounding behind the cavity in which the ripe ovum is lodged.
The aperture does not take the form of a funnel as in
Histriobdella; but, just in front of it on its dorsal side
is a prominent cushion-like body (cu.), the surface of which
is beset with stiff cilia vibrating sluggishly in the living
animal. In the cushion and around the aperture are nume-
rous nuclei and many muscular fibres.

The partition ($s.^2$), separating the cavity in which the
ripe ovum (with the rest of the ovary) lies from that out of
which the oviducts lead, is thickened towards the middle, and
produced into a pair of more or less prominent processes
projecting backwards and outwards into the cavity behind.
These thickenings, which vary greatly in different specimens,
contain a number of nuclei, together sometimes with rounded
bodies staining deeply with eosin. The proximity of these

to the oviducts and their cœlomic apertures suggests that
they may have some function in connection with the discharge
of the ovum.

In living specimens active movements of a remarkable
character were repeatedly observed to be taking place in the
largest ova. The appearance presented is that of a narrow
process being actively pushed inwards from the adjacent
tissues towards the centre of the ovum ; but since there is no
apparent mechanism present by which such an effect could
be produced, the movements must be the result of contrac-
tions of the substance of the ovum itself—probably of the
specialised superficial layer already referred to. The effect
of such movements is to bring the centrally placed nucleus
within easy reach of the periphery. Two ends might pre-
sumably be met by this peculiar change; the polar bodies
might be separated off without the nucleus being forced to
travel from its usual central position through a dense mass of
yolk-granules to the periphery, or the spermatozoon might
be at once received into the neighbourhood of the nucleus of
the ovum without having to perform a like journey.

Only in one case have I obtained sections of a specimen
fixed while such movements were going on. In this case it
was the second largest ovum—here thickly beset with yolk-
granules, in which, as observed also in a living specimen, the
phenomenon occurred. The ingrowth in this case reaches
from the outside nearly to the centre of the ovum, and appears
as a narrow fissure filled with cœlenchyme. The nucleus of
the ovum, situated near the bottom of this fissure, has become
modified ; it has become distended, the nuclear membrane has
almost disappeared though still traceable, and the chromatin
has become broken up into numerous small granules. Whether
the circumstance that in this specimen numerous spermatozoa
are to be detected fixed in the act of wandering through the
cœlenchyme in the immediate neighbourhood of the fissure in
the ovum has anything to do with the peculiar change in the
latter must remain undetermined. For the investigation of
this problem and the following out of the history of the

maturation and fertilisation, a much more abundant material is required than is at present available.

Masses of sperms are almost always to be found on each side in front of the third cirri and genital apertures. The appearances which these present vary very greatly. In one of the series of sections of the Tasmanian species previously described by me, the main mass of sperms is contained in what has the appearance of a case corresponding in form to a cast of the interior of the penis (6, pl. 15, fig. 12). This I supposed to be a spermatophore, and a re-examination of the sections strengthens the conclusion. In some series of sections of S. novæ-hollandiæ similar appearances are to be observed, though here the case of the spermatophore, if such it be, is rounded in form. In other series no trace of such a case appears. In one instance a stream of sperms is traceable backwards to the dorsal surface, where it is continued through the integument. It would thus appear that in the process of hypodermic impregnation the case of the spermatophore may or may not be passed into the interior of the impregnated female.

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EXPLANATION OF PLATES 11 to 14,[1]

Illustrating Professor W. A. Haswell's "Notes on the Histriobdellidæ."

LIST OF REFERENCE LETTERS.

b. Brain. *bd.* Bridle. *c.* Cœlenchyme. *c. c.* Caudal cœlenchyme. *ce. c.* Cervical cœlom. *ci.* Cirri. *cu.* Ciliated cushions. *f.* Fulcrum. *gl. c.* Cervical gland. *gl. d.* Dorsal gland. *h. c.* Head-cœlom. *i.* Intestine. *j.* Jaws. *l. gl.*[1]. Gland of anterior limb. *l. gl.*[2]. Gland of posterior limb. *l. j.* Lower jaw. *m. d.* Dorsal longitudinal muscles. *m. v.* Ventral longitudinal muscles. *n.*[1], *n.*[2], *n.*[3]. First, second and third pairs of nephridia. *n. c.* Nerve-cord. *o.* Ovary. *œ.* Œsophagus. *ov.*[1] Largest ovum. *ov.*[2]. Second largest ovum. *r.*[1], *r.*[2], *r.*[3], *r.*[4]. Ramules of upper jaw. *r. gl.* Rectal gland. *s.*[1]. Septum between neck-segment and trunk. *s.*[2]. Septum behind large ovum. *s.*[3]. Septum between trunk and tail. *s.*[4]. Partial segment in front of largest ovum. *s.*[5]. Septum between neck-segment and head. *sh.* Shell-gland secretion. *sh. gld.* Shell-gland. *st.* Stomach. *s. m.* Striated muscle (of jaws). *sp.* Spermatozoa. *sph.* Sphincter between œsophagus and stomach. *spp.* Spermatophore. *u. j.* Upper jaw. *v. m.* Vertical or dorso-ventral muscular fibres. *v. n.* " Visceral " nervous system. *vit.* Vitelline glands. ♀. Female genital aperture.

PLATE 11.

Figs. 1–5.—Five successive longitudinal vertical sections of a mature female Stratiodrilus novæ-hollandiæ. × 200. In the sections represented in figs. 1 and 4 the lower jaw (*l. j.*) has become detached from its natural position.

PLATE 12.

Fig. 6.—A sixth section of the same series as those represented in Plate 11. × 200.

[1] All the figures were re-drawn for me by Mr. F. W. Atkins.

Figs. 7–12.—Transverse sections of a mature female specimen of S. novæ-hollandiæ. × 600. The cilia of the enteric epithelium are not represented.

Fig. 7.—Section a little distance in front of the anterior end of the ovary with the posterior parts of the second pair of nephridia (n.²), the vitelline glands and the obliquely running longitudinal bands of cœlenchyme.

Fig. 8.—Section through the anterior part of the ovary with the loops of the third pair of nephridia (n³.) on the dorsal side of the ovary and the ventral side of the stomach.

Fig. 9.—Section immediately following that represented in fig. 8, with vertical septa enclosing a median space in which are the nerve-cord and the bends of the loops of the third pair of nephridia (n.³), which almost meet in the middle line.

Fig. 10.—Section passing through about the middle of the large ovum.

Fig. 11.—Section passing through one of the cirri of the third pair, and on the other side passing through the funnel or cushion (cu.) and the shell-gland secretion (sh.) in the neighbourhood of the genital aperture.

Fig. 12.—Section a little further back comprising the thickenings of the septum (s.²) behind the large ovum, shell-gland secretion (sh.) and the genital aperture (♀).

PLATE 13.

Fig. 13.—Transverse (slightly oblique) section through the head region at the bases of the anterior limbs. × 600.

Fig. 14.—Part of a transverse section from another series passing through the external genital aperture (♀), shell-glands (sh. gld.), ciliated cushion (cu.), with the large ovum (o.¹) and the thickening of the septum (s.²) behind it. × 500.

Fig. 15.—Section through the caudal region showing the relations of the cœlenchyme. × 600.

Fig. 16.—Anterior plates of lower jaw in S. tasmanicus. × 2400

Fig. 17.—Anterior plates of lower jaw of S. novæ-hollandiæ. × 2400.

Fig. 18.—Cirrus of posterior limb of S. novæ-hollandiæ.

Fig. 19.—Cirrus of posterior limb of S. tasmanicus.

Figs. 20–22.—Penis in S. novæ-hollandiæ.

Figs. 23–25.—Penis in S. tasmanicus.

PLATE 14.

Fig. 26.—Rami of upper jaw in S. novæ-hollandiæ partly everted with the parts slightly separated. × 2400.

Fig. 27.—Ramus of upper jaw of the same incompletely retracted, showing relations to lower jaw and bridle (represented by dotted outlines). × 2400.

Fig. 28.—Transverse section of longitudinal muscular fibres of Stratiodrilus showing the relations to the cœlenchyme. × 1500.

Fig. 29.—Longitudinal muscular fibres of an Enchytræid (from a transverse section) with muscle nuclei and a peritoneal nucleus; $c =$ cœlomic epithelium plus the myocyte layer. × 1500.